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Mortality, recruitment and growth of the tree communities in three forest formations at the Panga Ecological Station over ten years (1997-2007)[1]

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ABSTRACT

The area evaluated in this study was a continuous stretch comprising three vegetation formations: gallery forest, semideciduous seasonal forest and *cerradão* (woodland savanna). The aim of this study was to examine the tree community dynamics in a forest gradient—from gallery forest to *cerradão*—at Panga Ecological Station, in the city of Uberlandia, located in the state of Minas Gerais, Brazil. The study was based on data from a previous inventory of the continuous forest conducted in 211 permanent 10 × 10 m sample plots in eight parallel transect running perpendicular to Panga Creek. Trees with a diameter at breast height ≥ 4.77 cm were sampled in 1997, 2002 and 2007. With the exception of the *cerradão*, there was a net reduction in tree density over the studied period of ten years, because mortality rates were higher than the recruitment rates. The basal area increased during the period of the study, especially at *cerradão*. The mean mortality rate in the studied area was 2.64%.yr^{-1} and 3.36%.yr^{-1} for the 1997-2002 and 2002-2007 periods, respectively, whereas the mean recruitment rate was 1.76%.yr^{-1} and 1.97%.yr^{-1}, respectively. In general, mortality rates and recruitment rates have increased during the two successive periods of measurement and showed an imbalance in favor of mortality for the semideciduous seasonal forest and the gallery forest. This fact, added to the low density and high basal area, suggest that there was a process of thinning in the tree community. However, at *cerradão*, there was an imbalance in favor of recruitment, with a consequent increase in density and basal area, indicating that the *cerradão* is in a construction phase, which was further favored by a decrease in the occurrence of fire and other anthropogenic disturbances. When the turnover rates are taken into consideration, the global dynamics of the study area over the ten years evaluated can be expressed as *cerradão* > semideciduous seasonal forest > gallery forest.

Key words: Forest dynamics, gallery forest, semideciduous seasonal forest, woodland savanna, savanna

Introduction

Long-term studies on temporal changes in tropical forest remnants are necessary to make the distinction between natural dynamic processes and changes resulting from human activity (Korning & Balslev 1994a). Such studies can contribute to the prediction of forest growth and productivity, facilitating the implementation of management programs, as well as promoting the rational use and recovery of tropical forests (Carey *et al.* 1994). The changes that occur over time in tropical forests, in terms of their composition and structure, are the product of internal processes, such as competition for light (Harcombe *et al.* 2002), and external processes, such as climatic, geological and anthropogenic changes (Condit *et al.* 1992).

Forest communities that are free of anthropogenic disturbance display a dynamic equilibrium. Changes occur continuously over time at the individual and population levels, due to a balance among growth, recruitment and mortality (Hartshorn 1980; Swaine *et al.* 1987; Felfili 1995b), as well as local extinctions, immigration of new species and ecological drift (Condit *et al.* 1992). Therefore, these communities do not constitute a single equilibrium stage but a mosaic of successional stages, with arrays of species and individuals in different phases of regeneration, subjected to recurrent disturbances at varying frequencies (Hartshorn 1980).

Studies of the dynamics of tropical forests have been fundamental to the characterization and understanding of the diversity and complexity of plant populations and

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communities (Condit *et al.* 1992). With knowledge of the dynamic processes that modify the structure of a forest community, it is possible to infer the tendencies of a given ecosystem (Clark & Clark 1999) regarding changes in basal area, biomass and carbon balance (Lewis *et al.* 2009).

In tropical seasonal forests and in gallery forests subjected to annual climate seasonality, the rates of mortality and recruitment are higher than 3% per year (Paiva *et al.* 2007; Oliveira & Felfili 2008; Silva & Araújo 2009; Carvalho & Felfili 2011), whereas in wet forests these rates are lower, not exceeding 2% per year (Lang & Knight 1983; Manokaran & Kochummen 1987; Korning & Balslev 1994a; Rolim *et al.* 1999; Marques *et al.* 2009). Therefore, because of seasonality, together with functional and successional ecological processes (Murphy & Lugo 1986; Swaine *et al.* 1990), the community dynamics are more accelerated in seasonal and gallery forests than in wet forests.

The aim of this study was to detect the patterns of mortality, recruitment and growth of the tree community of a forest gradient—from gallery forest to semideciduous seasonal forest to *cerradão* (savanna woodland)—in two successive five-year intervals (1997-2002 and 2002-2007). These forest formations are subjected to pronounced seasonality in the rainfall distribution, with a long period of low precipitation (Oliveira-Filho & Ratter 2002). We tested the following hypotheses: because the study site has a seasonal climate, it displays accelerated dynamics, with high mortality and recruitment rates; and the dynamic processes are most intense in the *cerradão*, followed by the seasonal forest and the gallery forest.

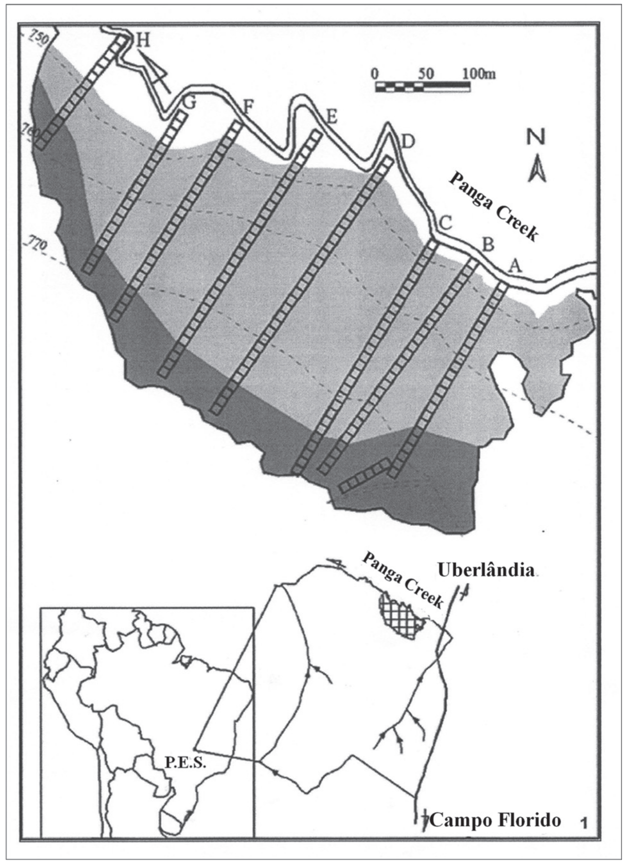

Figure 1. Location of the forest gradient, vegetation formations and transects studied at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil. Forest gradient: gallery forest (□), semideciduous forest (▒), *cerradão* (■); A to H: transects. Adapted from Moreno & Schiavini (2001).

Material and methods

Study site

The study site is located at the Panga Ecological Station (PES), near the city of Uberlândia, which is in the state of Minas Gerais, Brazil, and comprises three continuous forest formations: gallery forest (surrounding the Panga Creek), semideciduous seasonal forest and *cerradão* (Fig. 1). Until 1984, the area now occupied by the PES was extensively used as agricultural land (Cardoso & Schiavini 2002). The PES was acquired in 1986 by the Federal University of Uberlândia. It has a total area of 403.85 ha and is located approximately 30 km from Uberlândia (Schiavini & Araújo 1989). The vegetation of the PES consists of several vegetation formations found in the Cerrado (Savanna) Biome (*sensu* Ribeiro & Walter 2008), including forests, savannas and fields (Schiavini & Araújo 1989).

Within the PES, the gallery forest is distributed mainly along Panga Creek, which constitutes the northern border of the station, and, to a lesser extent, along the drainage channels and small streams in its southeast portion (Schiavini & Araújo 1989). Although the semideciduous seasonal forest is physiognomically similar to the gallery forest, it is located on an inclined relief, as an extension of the gallery forest, and possesses a characteristic flora (Schiavini & Araújo 1989). The *cerradão* is adjacent to the semideciduous seasonal forest, occupying a higher topographic position (Schiavini & Araújo 1989).

According to the Köppen classification system (Köppen 1948), the climate of the region is predominantly Aw type, with hot, humid summers and cold, dry winters (Alves & Rosa 2008). The mean annual precipitation is 1590 mm (± 247 mm), and the mean temperature is relatively uniform throughout the year. According to the Uberlândia Station of the 5th Meteorology District of the Brazilian Ministry of Agriculture and to the Climatology Station of the Federal University of Uberlândia, the wet season is from October to March and the dry season is from April to September.

The soil of all three forest formations has been classified as being of average texture and average acidity (pH 5.0-5.9), with low aluminum content in that of the semideciduous seasonal forest (Moreno & Schiavini 2001). According to Moreno & Schiavini (2001), the gradient of fertility for the study site, represented by the values for base saturation and sum of bases, follows the sequence semideciduous forest >

gallery forest > *cerradão*. The study site is located between elevations of 739 m and 773 m, thereabout, and the creek shows a mean declivity of approximately 0.18% (Cardoso & Schiavini 2002).

Continuous survey and data analysis

The survey was conducted in 211 permanent, 10 × 10 m sampling plots, in eight parallel transects running perpendicular to Panga Creek (Fig. 1). The transects end at the border between *cerradão* and *cerrado sensu stricto* (savanna). All individuals with a circumference at breast height ≥ 15 cm were sampled in 1997. The circumference data were transformed to diameter for the analyses employed in this study. In 2002 and 2007 the community was surveyed again, to record the growth (change in diameter), mortality and recruitment. The dataset from the surveys was used in order to calculate the demographic rates for both sampling periods (1997-2002 and 2002-2007).

The parameters of dynamics (mortality, recruitment and growth) were described for the study site as a whole, for each forest formation (gallery forest, semideciduous seasonal forest and *cerradão*) and for each vertical stratum (understory, midstory, overstory and emergent layer). The Shannon index (H') at the natural base was used as a measure of diversity and the Pielou index (J') was used as a measure of evenness, following Magurran (2004). The structure of the community was described in terms of number of individuals, basal area and distribution by diameter.

The classification of species according to their position in the vertical strata of the community was performed separately for each forest formation. The analysis of vertical stratification, adapted from Vale *et al.* (2009), was based on the height data for each species, with the aim to represent the true vertical position of the species (i.e., which stratum the species occupies when it reaches its maximum size) within the community. Only species with a minimum of ten individuals in the community in the 1997 survey were included in the analysis. The classification of strata considered the following criteria and intervals:

- understory ($Q3s \leq Mc$)
- midstory ($Mc < Q3s < Q3c$)
- overstory ($Q3s \geq Q3c \leq D9c$)
- emergent layer ($Q3s > D9c$)

where $Q3s$ and $Q3c$ are the third quartiles of the heights of individuals, within a species and within the community, respectively; Mc is the median height of the individuals sampled in the community; and $D9c$ is the ninth decile of the heights of the individuals sampled in the community.

The mean annual rates of mortality and recruitment were based on the logarithmic model (Swaine & Lieberman 1987). Because the basal area is also involved in the processes of mortality and recruitment, the mean annual rates of loss and gain in basal area of the individuals were estimated, as described by Werneck & Franceschinelli (2004). To express the global dynamics, the rate of turnover in number of individuals was calculated from the mean rates of mortality and recruitment, and the rate of turnover in basal area was calculated from the rates of loss and gain in basal area (Oliveira-Filho *et al.* 2007).

Growth is usually expressed in terms of diameter and basal area. Diameter is the main determinant of basal area, which justifies the preference for expressing growth in terms of diameter (Braga & Rezende 2007). The annual diameter increment (ADI) expresses the annual growth of an individual and is based on the difference in diameter between two periods, divided by the time in years between the two measurements (Finger 1992). The mean increments were calculated for the surviving trees between the periods of 1997-2002 and 2002-2007. In calculating the mean ADI, we converted each of the negative ADIs recorded for some individuals to zero, thus assuming that there was no growth in the period, as adopted by Felfili (1995b). The negative ADIs represented less than 0.01% of the ADIs analyzed in the community.

The differences in the rates of mortality and recruitment among the vertical strata for each period were determined by the Kruskal-Wallis test, followed by the median test for multiple comparisons among the strata (Zar 2010). The median test quantifies the number of times each stratum appears above or below the median and compares this with the chi-square distribution in a contingency table of expected and observed values. The Wilcoxon nonparametric test was used in order to compare the two measurement periods (1997-2002 and 2002-2007) in terms of the mean rates of mortality and recruitment for each stratum (Zar 2010). The statistical analyses were performed at the 5% significance level with the Systat program, version 10.2 (Wilkinson 1990).

Results

In 1997, the forest gradient showed a total of 3797 individuals, with a basal area of 23.95 m^2/ha (Table 1). In general, the results suggest a net reduction in density over the studied period of ten years (Tab. 1), because mortality rates were higher than were recruitment rates (Tab. 2), the only exception being the *cerradão*. The basal area of the gradient increased during the study period, especially for the *cerradão* (Tab. 1). As for the floristic composition, the number of species declined over the study period. The fluctuation in the number of species in the community is due to the entry and exit of rare species (n < 2), which did not alter the estimated values of diversity and evenness (Tab. 1). The same was observed for the botanical families. Among the rare species removed from the floristic list in the gradient are those whose occurrence was restricted to the *cerradão* and those that are typical of the adjacent area of *cerrado sensu stricto* (Appendix 1).

The forest gradient showed mortality rates of 2.64%.year^{-1} and 3.36%.year^{-1} for the periods of 1997-2002 and

Table 1. Characteristics of the forest gradient and its vegetation formations in 1997, 2002 and 2007 at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil.

Variable	Gallery forest (0.21 ha)			Semideciduous forest (1.5 ha)			*Cerradão* (0.4 ha)			Entire gradient (2.11 ha)		
	1997	2002	2007	1997	2002	2007	1997	2002	2007	1997	2002	2007
Families, n	30	31	29	41	41	40	41	40	40	51	50	48
Species, n	60	62	58	113	116	113	97	95	92	162	160	151
Diversity (H')	3.60	3.60	3.54	3.79	3.84	3.84	3.81	3.79	3.73	4.13	4.15	4.12
Evenness (J')	0.88	0.87	0.87	0.80	0.81	0.81	0.83	0.83	0.83	0.81	0.82	0.82
Basal area (m^2)	4.99	5.58	5.51	32.02	32.74	32.53	8.33	9.64	10.13	45.77	47.97	48.17
Basal area ($m^2.ha^{-1}$)	23.76	26.57	26.24	21.35	21.83	21.69	20.83	24.10	25.33	21.69	22.73	22.83
Density (n of individuals)	356	349	315	2514	2344	2170	927	985	1005	3797	3678	3490
Density (n of individuals.ha^{-1})	1695	1662	1500	1676	1563	1447	2318	2463	2513	1800	1743	1654

Table 2. Parameters of the dynamics in the forest gradient and its vegetation formations over a period of ten years at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil.

Parameter	Gallery forest		Semideciduous forest		*Cerradão*		Entire gradient	
	1997-2002	2002-2007	1997-2002	2002-2007	1997-2002	2002-2007	1997-2002	2002-2007
M (%.$year^{-1}$)	2.13	3.03	3.02	3.64	1.83	2.83	2.64	3.36
R (%.$year^{-1}$)	1.57	0.84	1.40	1.76	2.79	2.83	1.76	1.97
T_N (%.$year^{-1}$)	1.92	1.98	2.29	2.83	2.41	2.99	2.29	2.80
L (%.$year^{-1}$)	1.81	2.15	2.07	2.37	1.07	2.30	1.84	2.33
G (%.$year^{-1}$)	0.62	1.76	2.33	2.04	3.88	2.88	2.59	2.21
T_{BA} (%.$year^{-1}$)	1.21	1.96	2.20	2.20	2.47	2.59	2.21	2.27

M – mean annual mortality; R – mean annual recruitment; T_N – turnover in number of individuals; L – loss in basal area (outgrowth); G – gain in basal area (in-growth); T_{BA} – turnover in basal area.

2002-2007, respectively. The recruitment rates for the same period were 1.76%.$year^{-1}$ and 1.97%.$year^{-1}$, respectively. Between the two periods, the mortality and recruitment rates increased for all of the vegetation formations studied, except for the gallery forest, which showed a decrease in the recruitment rate (Tab. 2). All formations except the *cerradão* showed an imbalance in favor of mortality. Recruitment rates were higher in the *cerradão*: approximately 3% per year.

The semideciduous seasonal forest showed the greatest reduction in basal area for both measurement periods, due to the death of large trees, whereas the greatest gain, due to high recruitment, was in the *cerradão* (Tab. 2). When the turnover rates are taken into consideration, the global dynamics of the study area over the ten years evaluated can be expressed as *cerradão* > semideciduous seasonal forest > gallery forest.

The species evaluated in the analysis of the vertical structure represented 92% and 41% of the number of individuals and the number of species of the tree community, respectively. From 1997 to 2007, the species of the overstory and midstory dominated the gradient, followed by the species of understory and emergent layer (Tab. 3). There was no change in the proportional distribution of species among the strata over the course of the study period.

In general, only the species of the emergent layer showed mortality rates below the mean of the forest gradient and lower than those of the remaining strata (Fig. 2). However, the difference was significant only for the 2002-2007 period (Kruskal-Wallis, $H_{3,67} = 8.66$; $p = 0.03$), the emergent layer showing lower mortality than did the understory (median test, $z = 2.87$; $p = 0.02$). Only the understory showed mean annual recruitment rates above those found for the forest community in both measurement periods (Fig. 2). A significant difference among the strata was observed only for recruitment rates in the 2002-2007 period (Kruskal-Wallis, $H_{3,67} = 10.70$; $p = 0.01$), the understory showing higher recruitment than did the overstory (median test, $z = 2.81$; $p = 0.03$).

Only the overstory showed a significant increase in mortality rates from the 1997-2002 period to the 2002-2007 period (Wilcoxon, $Z = 3.42$; $p = 0.001$). The overstory was also the only stratum to show a significant decrease in recruitment rates along these same periods (Wilcoxon, $Z = 2.25$; $p = 0.002$).

Table 3. Changes in the distribution of species and individuals with higher density (n > 10) over a period of ten years (1997 to 2007), for each stratum of the forest gradient at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil. Numbers between parentheses are percentages in the strata.

Stratum	Number of individuals						Number of species	
	1997		2002		2007		1997 to 2007	
Understory	683	(19.5)	684	(20.3)	729	(22.9)	14	(20.9)
Midstory	1079	(30.9)	1024	(30.4)	946	(29.8)	17	(25.4)
Overstory	1492	(42.7)	1420	(42.1)	1250	(39.3)	29	(43.3)
Emergent layer	241	(6.9)	242	(7.2)	254	(8.0)	7	(10.4)
Total	3495		3370		3179		67	

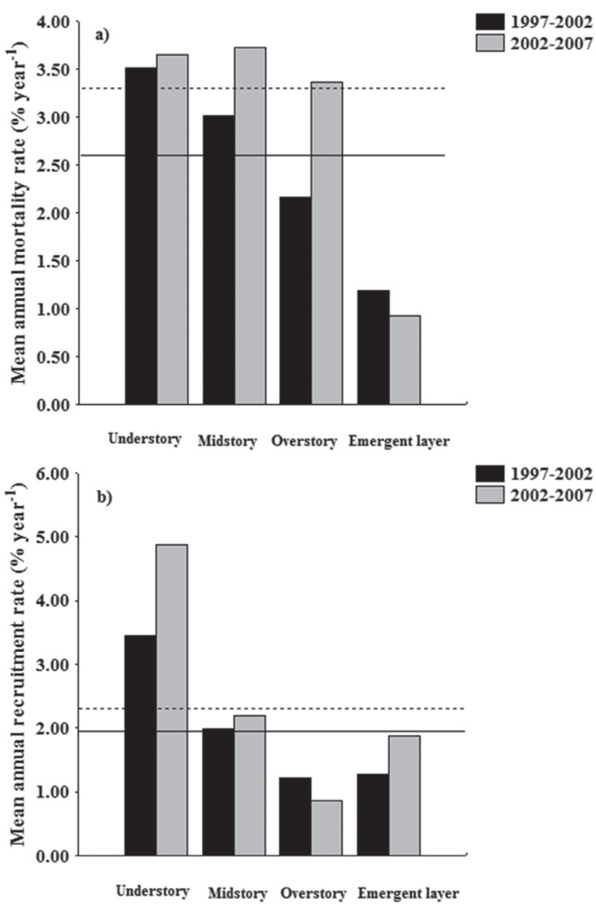

Figure 2. Mean annual rates of mortality and recruitment of the tree species in the vertical strata of the forest gradient at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil, at the periods of 1997-2002 and 2002-2007. Solid and dashed lines represent the annual rates of the forest gradient in the 1997-2002 and 2002-2007 periods, respectively.

The mean ADIs of the forest gradient in the periods of 1997-2002 and 2002-2007 were 0.15 and 0.13 cm.year^{-1}, respectively. The variation between the two measurement periods, in terms of the ADIs calculated (Tab. 4), was high: 131% and 150% in the in the 1997-2002 and 2002-2007 periods, respectively. The median ADIs were much lower than were the means, showing a higher uniformity among the vegetation formations, except for the *cerradão* in the 1997-2002 period (Tab. 4). However, in the 2002-2007 period, the difference in the ADIs was altered in the sequence *cerradão* = gallery forest > semideciduous forest. The results of the Kruskal-Wallis test (H) and of the median test (z) for multiple comparisons among the vegetation formations are shown in Tab. 5.

Discussion

Over the ten-year period of monitoring in the gradient studied, we observed a reduction in tree density and an increase in basal area for the semideciduous forest and gallery forest. Similar patterns have been documented in other studies of gallery forests and semideciduous seasonal forests, as well as in those of areas of tropical forest, Atlantic Forest and deciduous forest (Tab. 6). According to Finegan (1996) and Guariguata & Ostertag (2001), over the course of the successional process, density tends to decrease in parallel with the increasing age of the forest, a pattern cited as one of the main characteristics of forest succession. The process of increasing basal area and decreasing tree density, also known as self-thinning (Oliveira-Filho *et al.* 1997), consists of the growth and accumulation of biomass by a few trees that survive intraspecific and interspecific competition, coupled with the mortality of various individuals, most with small diameters (Machado & Oliveira-Filho 2010). Thus, the forest gradient tends to change from a community with high density of individuals to a community characterized by low tree density and increase in biomass by the individuals with larger size. This tendency, as observed here, is explained by the fact that the forest gradient is inserted in a protected area, with no occurrence of disturbances in the last 30 years.

The concomitant increase in basal area and density observed in the *cerradão* has also been reported for other areas of *cerrado sensu stricto* in Brazil (Henriques & Hay 2002; Libano & Felfili 2006; Roitman *et al.* 2008). The structure and composition of cerrado areas protected from fire have changed significantly over the years (Moreira 2000; Durigan & Ratter 2006; Cardoso *et al.* 2009), as, for example, the increases in density, basal area and number of species (19%, 15% and 35%, respectively) reported for a *cerrado* in southeastern Brazil that was protected from fire (Roitman *et al.*

Table 4. Mean and median of the annual diameter increment of the forest gradient and its vegetation formations at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil, for the periods of 1997-2002 and 2002-2007.

Statistic	Gallery forest		Semideciduous forest		*Cerradão*		Gradient	
	1997-02	2002-07	1997-2002	2002-07	1997-02	2002-07	1997-02	2002-07
Mean (cm)	0.14	0.13	0.14	0.12	0.19	0.15	0.15	0.13
CV (%)	131	153	136	161	118	129	131	150
Median (cm)	0.06	0.06	0.06	0.03	0.13	0.06	0.06	0.06
N	320	300	2162	1954	846	855	3328	3109

CV – coefficient of variation; N – number of surviving individuals.

Table 5. Results of the median test (z) for multiple comparisons of the annual diameter increment among the vegetation formations for the periods of 1997-2002 ($H_{3,6656}$ = 41.38; p = 0.001) and 2002-2007 ($H_{3,6218}$ = 37.31; p = 0.001) at the Panga Ecological Station, in the city of Uberlândia, state of Minas Gerais, Brazil. Values with asterisk show a significant difference ($p \leq 0.05$).

1997 to 2002					2002 to 2007				
Formation	GF	C	SF	FG	Formation	GF	C	SF	FG
GF	-	3.279*	0.663	0.494	GF	-	1.972	1.743	0.521
C	3.279*	-	6.285*	4.838*	C	1.972	-	5.862*	4.243*
SF	0.663	6.285*	-	2.484	SF	1.743	5.862*	-	2.651*
FG	0.494	4.838*	2.484	-	FG	0.521	4.243*	2.651*	-

GF – gallery forest; C – *cerradão*; SF – semideciduous forest; FG – forest gradient.

Table 6. Structural and demographic parameters of successive monitoring studies in permanent plots in tropical forest formations.

Author	Vegetation	Inclusion limit	Period	Basal area ($m^2.ha^{-1}$)	Mortality (%.year^{-1})	Recruitment (%.year^{-1})	Growth (mean)
(Korning & Balslev 1994a)	Tropical wet forest	10 cm	4.9 years	27.2-28.9	1.88	1.78	9.3 cm^2
(Korning & Balslev 1994a)	Tropical wet forest	10 cm	2.5 years	22.2-24.0	1.04	3.09	13.6 cm^2
(Korning & Balslev 1994b)	Tropical wet forest	10 cm	1983-1990	-	-	-	0.1 to 0.55 cm.year-1
(Lang & Knight 1983)	Tropical wet forest	2.5 cm	1968-1978	25.7-31.4	2.23	0.86	0.1 to 1.5 cm.year-1
(Manokaran & Kochummen 1987)	Tropical wet forest	10 cm	1947-1981	32.4	2.02	-	0.08 to 0.49 cm.year-1
(Rolim *et al.* 1999)	Atlantic Forest	10 cm	1980-1995	-	1.5	1.5	-
(Marques *et al.* 2009)	Atlantic Forest - non floodable	4.4 cm	1991-2007	23.7-27.0	1.3	2.1	5.24 (10-3 cm.cm2.year-1)
(Marques *et al.* 2009)	Atlantic Forest - floodable	4.4 cm	1991-2007	37.0-38.5	2	1.6	9.07 (10-3 cm.cm2.year-1)
(Gomes *et al.* 2003)	Atlantic Forest	8 cm	1989-1995	17.0-19.5	1.67	3.46	0.28 to 1.44 %.year-1
(Felfili 1995b)	Gallery forest	10 cm	1985-1991	30.4	3.5	2.7	0.25 cm.year-1
(Braga & Rezende 2007)	Gallery forest	5 cm	1994-2005	-	5.55	1.42	0.20 cm.year-1
(Oliveira-Filho *et al.* 1997)	Semideciduous forest	5 cm	1987-1992	18.8-21.5	2.56	2.99	1.43 cm.year-1
(Paiva *et al.* 2007)	Semideciduous forest	5 cm	1989-2000	-	4.1	4.04	-
(Silva & Araújo 2009)	Semideciduous forest	3.18 cm	1990-2004	28.8-26.84	4.1	4.5	-
(Swaine *et al.* 1990)	Deciduous forest	10 cm	1979-1987	-	2.38	1.5	1 to 3.5 %.year^{-1}
(Carvalho 2009)	Deciduous forest	5 cm	2000-2006	14.9-16.5	2.77	4.43	0.25 cm.year-1
(Werneck & Franceschinelli 2004)	Deciduous forest	3.2 cm	1994-1998	23.7-24.2	5	2.1	-
(Werneck & Franceschinelli 2004)	Deciduous forest	10 cm	1994-1998	19.5-20.4	2.3	2.3	-
(Roitman *et al.* 2008)	*Cerrado sensu stricto*	5 cm	1991-2004	8.1-9.2	1.93	3.72	0.096 cm.year-1
THIS STUDY	Gallery forest	4.8 cm	1997-2007	23.8-26.2	2.11 and 2.98	1.72 and 0.97	0.14 and 0.13 cm.year-1
	Semideciduous forest	4.8 cm	1997-2007	21.4-21.7	2.97 and 3.57	1.60 and 2.08	0.14 and 012 cm.year-1
	Cerradão	4.8 cm	1997-2007	20.9-25.3	1.81 and 2.79	3.00 and 3.18	0.19 and 0.15 cm.year-1
	Entire forest gradient	4.8 cm	1997-2007	21.7-22.8	2.60 and 3.31	1.98 and 2.29	0.15 and 0.13 cm.year-1

2008). The pattern of increase in both density and basal area recorded in the *cerradão* studied here seems to be related to a decrease in the incidence of fire and of anthropogenic disturbances at the Panga Ecological Station.

The Shannon diversity indices found for all of the vegetation formations studied here (H' > 3.5) are within the range reported for other semideciduous forests in Brazil (Silva *et al.* 2004; Vale *et al.* 2009; Dias Neto *et al.* 2009; Prado-Júnior *et al.* 2010), as well as for other areas of *cerradão* (Pereira-Silva *et al.* 2004; Fina & Monteiro 2009). The final value calculated for the forest gradient as a whole (H' > 4.10) is close to that observed for tropical forests (Knight 1975) and reflects the environmental heterogeneity of the forest gradient, which is related to the edaphic gradient (Moreno & Schiavini 2001) and to the topographic gradient (Cardoso & Schiavini 2002). Between the two measurement periods, there were minor changes in the floristic composition, related to the exit of rare species, often restricted to the *cerradão*, which forms the border with an area of *cerrado sensu stricto*. In general, the entry and exit of species in forest formations is observed for species with low abundance (Kellman *et al.* 1998; Nascimento *et al.* 1999; Pinto & Hay 2005).

The mean annual mortality rate of 2.64% calculated for the forest gradient for the 1997-2002 period (Tab. 6) is within the range of 2-3% per year reported for tropical forests (Manokaran & Kochummen 1987; Korning & Balslev 1994a) and deciduous forests (Swaine *et al.* 1990; Carvalho & Felfili 2011), as well as for other semideciduous seasonal forests (Oliveira-Filho *et al.* 1997) and gallery forests (Pinto & Hay 2005). The rate observed in the 2002-2007 period, approximately 3% per year, is also comparable to that reported in more recent studies of deciduous forests (Werneck & Franceschinelli 2004; Marin *et al.* 2005), semideciduous seasonal forests (Nascimento *et al.* 1999; Paiva *et al.* 2007; Silva & Araújo 2009; Machado & Oliveira-Filho 2010) and gallery forests (Felfili 1995b; Oliveira & Felfili 2008). The variation in mortality rates over time can be related to factors such as climatic stresses (Slik 2004), longevity of the species that compose the community (Manokaran & Kochummen 1987; Felfili 1995a), anthropogenic disturbances (Gomes *et al.* 2003; Werneck & Franceschinelli 2004) and successional stage of the forest.

The annual recruitment rate found for the gradient (2.6-3.31% per year) is similar to the 2-3.5% per year reported for other semideciduous forests (Oliveira-Filho *et al.* 1997; Appolinário *et al.* 2005; Oliveira-Filho *et al.* 2007) and gallery forests (Felfili 1995a; Oliveira & Felfili 2008), as well as for deciduous forests (Werneck & Franceschinelli 2004). However, more recently, rates > 4% per year have been reported, having been attributed to post-disturbance recovery, in a semideciduous forest (Silva & Araújo 2009), and to increased rainfall, in a deciduous forest (Carvalho & Felfili 2011).

In general, the rates of mortality and recruitment increased between the two successive measurement periods evaluated in the present study. For the semideciduous seasonal forest and the gallery forest, the imbalance in favor of mortality, the decrease in density and the increase in basal area suggest a process of self-thinning in the tree community. In the *cerradão*, however, the positive balance in favor of recruitment and the increases in density and basal area indicate that this vegetation formation is in the construction phase, which is favored by the decrease in the occurrence of fire and other anthropogenic disturbances (Cardoso *et al.* 2009), resulting in the expansion of the *cerradão* into areas of *cerrado sensu stricto* and in some areas of *cerradão* being supplanted by semideciduous forest.

There were no significant differences among the strata in terms of the mean annual rates of recruitment and mortality. We can highlight only the emergent layer, which had a lower mortality rate than did the understory, and the understory, which had a higher recruitment rate than did the overstory. The tendency for the mortality rate to be lower in the emergent layer than in the understory has also been found in studies of tropical forests. Manokaran & Kochummen (1987) reported differences in the mortality rates among groups of species in forests of dipterocarps in the sequence emergent layer < overstory < understory < shade-intolerant species. In tropical forests, the mean annual mortality rate has also been shown to decrease in parallel with increasing tree height, understory species showing the highest rate, followed by those of the midstory and overstory (Lang & Knight 1983; Korning & Balslev 1994b). According to Turner (2001), understory species show high mortality due to the risk of large trees falling and to competition; therefore, these species should recruit more individuals than do overstory species, which grow faster and are more efficient in escaping the limiting conditions of the understory.

The ADIs recorded for the forest gradient in the two measurement periods were comparable to those obtained for some tropical wet forests in the Amazon (Uhl *et al.* 1988; Laurance *et al.* 1998) and lower than those obtained for tropical forests (Lieberman *et al.* 1985), gallery forests (Felfili 1995b; Braga & Rezende 2007; Oliveira & Felfili 2008) and deciduous forests (Carvalho & Felfili 2011). These values are typical of undisturbed forests, values > 0.3 $cm.year^{-1}$ being found in disturbed environments, which are subjected to timber exploitation (Silva *et al.* 1995) or display an edge effect with a predominance of pioneer and heliophytic species (Pulz 1998).

The forest gradient studied here, especially the *cerradão*, showed high rates of mortality and recruitment, confirming the pattern found in the forest formations subjected to climatic seasonality and having had no recent anthropogenic disturbances, because they are located in a protected area. These results suggest that the forest gradient studied is in the self-thinning phase, especially the semideciduous seasonal forest and the gallery forest, which showed a decrease in density and an increase in basal area. The *cerradão*, however, showed higher ADIs than did the other vegetation formations studied, probably because of the higher recruitment, which, in addition to the increase in basal area and tree density, suggests that this vegetation formation is in the construction phase.

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Appendix 1. List of the tree species within the forest gradient studied at the Panga Ecological Station in Brazil. The species are shown in alphabetical order by botanical family (53 families comprising 165 species), followed by their respective occurrences in the vegetation formations during the interval from 1997 to 2007.

FAMILY	Occurrence			N		
Species	C	SF	GF	1997	2002	2007
ANACARDIACEAE						
Astronium fraxinifolium Schott ex Spreng.	X	X		6	6	6
Lithraea molleoides (Vell.) Engl.	X	X	X	84	48	25
Tapirira guianensis Aubl.	X	X	X	102	110	103
ANNONACEAE						
Annona crassiflora Mart.	X			3	3	3
Cardiopetalum calophyllum Schltdl.	X	X		7	10	4
Duguetia lanceolata A.St.-Hil.			X	1	1	1
Unonopsis lindmanii R.E.Fr.		X	X	4	6	8
Xylopia aromatica (Lam.) Mart.	X	X		28	38	43
APOCYNACEAE						
Aspidosperma cuspa (Kunth) S.F.Blake ex Pittier	X	X	X	97	94	91
Aspidosperma cylindrocarpon Müll.Arg.	X	X	X	43	48	47
Aspidosperma olivaceum Müll.Arg.		X		10	12	9
Aspidosperma parvifolium A.DC.		X		26	26	23
Aspidosperma subincanum Mart. ex A.DC.	X	X		32	30	28
ARALIACEAE						
Dendropanax cuneatus (DC.) Decne. & Planch.		X	X	11	13	14
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	X			2	1	1
ARECACEAE						
Acrocomia aculeata (Jacq.) Lodd. ex Mart.		X		8	7	7
Syagrus flexuosa (Mart.) Becc.	X			1	1	1
ASTERACEAE						
Piptocarpha rotundifolia (Less.) Baker	X			1	-	-
BIGNONIACEAE						
Cybistax antisyphilitica (Mart.) Mart.	X			1	1	1
Handroanthus impetiginosus (Mart. Ex DC) Mattos	X	X		3	2	2
Handroanthus umbellatus (Sonder) Mattos	X		X	5	5	4
Tabebuia roseoalba (Ridl.) Sandwith	X	X	X	22	22	21
BORAGINACEAE						
Cordia alliodora (Ruiz & Pav.) Oken		X		1	1	1
Cordia sp.	X	X		6	5	4
BURSERACEAE						
Protium heptaphyllum (Aubl.) Marchand		X	X	43	45	51
CANNABACEAE						
Celtis iguanaea (Jacq.) Sarg.		X		2	2	1
CARYOCARACEAE						
Caryocar brasiliense Cambess.	X			2	-	-

FAMILY	Occurrence			N		
Species	C	SF	GF	1997	2002	2007
CELASTRACEAE						
Cheiloclinium cognatum (Miers.) A.C.Sm.		X	X	7	7	8
Maytenus floribunda Reissek	X	X		40	44	46
Plenckia populnea Reissek	X			4	4	2
CHRYSOBALANACEAE						
Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook.f.	X			1	1	1
Hirtella gracilipes (Hook.f.) Prance	X			1	2	3
Licania humilis Cham. & Schltdl.	X			1	1	1
CLUSIACEAE						
Calophyllum brasiliense Cambess.			X	12	18	16
Garcinia brasiliensis Mart.		X		2	2	3
Kielmeyera coriacea Mart. & Zucc.	X			1	1	-
COMBRETACEAE						
Terminalia argentea (Cambess.) Mart.	X	X		6	6	6
Terminalia glabrescens Mart.	X	X	X	65	64	68
Terminalia phaeocarpa Eichler	X	X		52	53	44
CONNARACEAE						
Connarus suberosus Planch.	X			4	1	1
EBENACEAE						
Diospyros burchellii Hiern.	X			14	16	15
Diospyros hispida A.DC.	X	X		198	195	170
ERYTHROXYLACEAE						
Erythroxylum deciduum A.St.-Hil.		X	X	14	9	7
EUPHORBIACEAE						
Croton urucurana Baill.		X	X	3	1	-
FABACEAE						
Acacia polyphylla DC.	X	X		10	10	11
Acosmium subelegans (Mohlenbr.) Yakovlev	X			16	15	9
Agonandra brasiliensis Miers ex Benth. & Hook.	X	X		2	3	3
Albizia niopoides (Spruce ex Benth.) Burkart		X		2	2	3
Anadenanthera colubrina (Vell.) Brenan	X	X	X	110	108	105
Apuleia leiocarpa (Vogel) J.F.Macbr.		X		2	2	2
Bauhinia ungulata L.	X	X	X	21	20	17
Bowdichia virgilioides Kunth	X			8	8	6
Copaifera langsdorffii Desf.	X	X	X	46	50	56
Dalbergia miscolobium Benth.	X			1	1	1
Dimorphandra mollis Benth.	X			2	1	1
Enterolobium gummiferum (Mart.) J.F.Macbr.	X			1	1	-
Hymenaea courbaril L.		X	X	22	21	21

FAMILY	Occurrence			N		
Species	C	SF	GF	1997	2002	2007
Inga laurina (Sw.) Willd.		X		2	2	2
Inga marginata Willd.		X	X	2	2	1
Inga vera Willd.		X	X	17	17	13
Lonchocarpus cultratus		X		2	2	2
Machaerium acutifolium Vogel	X	X		50	47	40
Machaerium brasiliense Vogel		X		9	12	12
Machaerium hirtum (Vell.) Stellfeld	X	X	X	46	43	35
Machaerium stipitatum (DC.) Vogel		X		8	8	8
Ormosia arborea (Vell.) Harms		X		1	2	2
Piptadenia gonoacantha (Mart.) J.F.Macbr.		X		6	4	4
Platypodium elegans Vogel	X	X	X	40	42	40
Senna silvestris (Vell.) H.S.Irwin & Barneby	X	X	X	8	8	7
Stryphnodendron polyphyllum Mart.	X			1	-	-
Sweetia fruticosa Spreng.		X		9	11	13
LACISTEMACEAE						
Lacistema aggregatum (P.J.Bergius) Rusby	X			-	1	1
LAMIACEAE						
Aegiphila sellowiana Cham.		X		1	1	1
LAURACEAE						
Aniba heringeri Vattimo-Gil			X	4	3	3
Endlicheria paniculata (Spreng.) J.F.Macbr.		X	X	23	18	18
Lauraceae 1			X	1	1	1
Lauraceae 2	X			1	-	-
Nectandra cissiflora Nees		X	X	32	33	41
Ocotea corymbosa (Meisn.) Mez	X	X	X	11	8	12
Ocotea minarum (Nees) Mez	X	X		15	17	16
Ocotea percoriacea (Meisn.) Kosterm.			X	1	-	-
Ocotea pulchella Mart.	X	X	X	43	32	19
LECYTHIDACEAE						
Cariniana estrellensis (Raddi) Kuntze		X		10	10	10
LOGANIACEAE						
Strychnos pseudoquina A.St.-Hil.	X			1	-	-
MAGNOLIACEAE						
Magnolia ovata (A.St.-Hil.) Spreng.			X	8	7	6
MALPIGHIACEAE						
Byrsonima crassa Nied.	X			2	1	1
Byrsonima sp	X			1	1	1
MALVACEAE						
Apeiba tibourbou Aubl.		X		2	2	2
Eriotheca candolleana (K.Schum.) A.Robyns		X		6	6	7

FAMILY	Occurrence			N		
Species	C	SF	GF	1997	2002	2007
Eriotheca gracilipes (K.Schum.) A.Robyns	X			1	1	-
Guazuma ulmifolia Lam.	X	X	X	83	60	37
Luehea divaricata Mart.		X	X	28	24	23
Luehea grandiflora Mart. & Zucc.	X	X		91	91	96
Pseudobombax tomentosum (Mart. & Zucc.) A.Robyns	X	X		6	5	5
MELASTOMATACEAE						
Miconia albicans (Sw.) Triana	X			4	6	8
Miconia calvescens Schrank & Mart. ex DC.		X		1	1	-
MELIACEAE						
Guarea kunthiana A.Juss.			X	1	1	1
Trichilia catigua A.Juss.	X			1	1	1
Trichilia elegans A.Juss.		X		-	-	1
Trichilia pallida Sw.		X	X	5	7	7
MORACEAE						
Brosimum gaudichaudii Trécul	X	X		3	3	1
Ficus enormis (Mart. ex Miq.) Mart.	X			1	1	1
Maclura tinctoria (L.) Steud.		X		1	1	-
MYRISTICACEAE						
Virola sebifera Aubl.	X	X		2	2	7
MYRSINACEAE						
Myrsine coriacea (Sw.) Roem. & Schult.	X	X	X	15	15	10
Myrsine umbellata Mart.	X	X		60	61	45
MYRTACEAE						
Calyptranthes widgreniana O.Berg			X	10	9	6
Campomanesia velutina (Cambess.) O.Berg		X		139	101	63
Eugenia aurata O.Berg	X			1	1	1
Eugenia florida DC.	X	X	X	20	22	22
Eugenia involucrata DC.		X		16	23	25
Eugenia ligustrina (Sw.) Willd.		X	X	9	9	13
Myrcia castrensis (O. Berg) D. Legrand			X	1	1	-
Myrcia laruotteana Cambess.			X	1	1	-
Myrcia splendens (Sw.) DC.	X	X		66	45	31
Myrcia tomentosa (Aubl.) DC.	X	X		39	40	40
Myrcia variabilis DC.	X			2	1	-
Psidium rufum DC.		X		5	5	5
Psidium sartorianum (O.Berg) Nied.		X		5	5	8
Psidium sp		X		4	4	4
NYCTAGINACEAE						
Guapira noxia (Netto) Lundell	X			2	2	2
Guapira venosa		X		2	2	3

FAMILY	Occurrence			N		
Species	C	SF	GF	1997	2002	2007
Neea hermaphrodita S.Moore			X	2	2	2
OCHNACEAE						
Ouratea castaneifolia (DC.) Engl.	X	X		10	10	12
OLACACEAE						
Heisteria ovata Benth.				-	1	1
OLEACEAE						
Chionanthus trichotomus (Vell.) P.S.Green		X	X	11	13	13
PHYLLANTHACEAE						
Margaritaria nobilis L.f.		X		2	2	3
Phyllanthus acuminatus Vahl		X		1	1	2
PICRAMNIACEAE						
Picramnia sellowii Planch.			X	1	1	-
POLYGONACEAE						
Coccoloba mollis Casar.	X	X		3	3	2
PROTEACEAE						
Roupala brasiliensis Klotzsch	X	X		23	22	21
Roupala montana Aubl.	X	X		28	27	25
Rhamnidium elaeocarpum Reissek	X	X	X	53	45	36
ROSACEAE						
Prunus selowi	X			3	2	1
RUBIACEAE						
Cordiera sessilis	X	X	X	193	237	327
Coussarea hydrangeifolia (Benth.) Müll.Arg.	X	X	X	43	68	84
Coutarea hexandra (Jacq.) K.Schum.		X		3	3	3
Faramea nigrescens Mart.	X	X	X	20	35	50
Guettarda viburnoides Cham. & Schltdl.	X	X		50	45	40
Ixora gardneriana Benth.			X	1	1	1
Rudgea viburnoides (Cham.) Benth.	X	X		36	37	44
Simira viridiflora (Allemão & Saldanha) K.Schum.		X		5	6	5
Tocoyena formosa (Cham. & Schltdl.) K.Schum.		X		1	2	2
SALICACEAE						
Casearia gossypiosperma Briq.	X	X		7	7	7
Casearia rupestris Eichler		X	X	15	13	12
Casearia sylvestris Sw.	X	X	X	83	82	68
Prockia crucis P.Browne ex L.		X		1	4	3
SAPINDACEAE						
Allophylus sericeus		X		2	1	1
Cupania vernalis Cambess.	X	X		112	77	65
Dilodendron bipinnatum Radlk.		X		22	19	18
Matayba elaeagnoides Radlk.	X	X	X	60	65	64

FAMILY	Occurrence			N		
Species	C	SF	GF	1997	2002	2007
Matayba guianensis Aubl.	X	X	X	185	173	165
SAPOTACEAE						
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	X	X	X	309	274	222
Pouteria gardneri (Mart. & Miq.) Baehni	X	X		13	13	13
Pouteria torta (Mart.) Radlk.		X		8	10	11
SIPARUNACEAE						
Siparuna guianensis Aubl.	X			2	7	15
STYRACACEAE						
Styrax camporum Pohl	X	X	X	74	65	56
Styrax ferrugineus Nees & Mart.	X			1	1	1
SYMPLOCACEAE						
Symplocos pubescens Klotzsch ex Benth.	X	X	X	23	26	26
URTICACEAE						
Cecropia pachystachya Trécul	X	X	X	9	8	10
VOCHYSIACEAE						
Qualea dichotoma (Mart.) Warm.	X	X	X	8	10	10
Qualea grandiflora Mart.	X	X		89	85	82
Qualea multiflora Mart.	X			3	3	1
Qualea parviflora Mart.	X			4	4	3
Vochysia tucanorum Mart.	X	X	X	71	72	54

C – *cerradão*; SF – semideciduous forest; GF – gallery forest.